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Searching for generality in the patterns of parasite abundance and distribution: Ectoparasites of a South African rodent, *Rhabdomys pumilio*

Sonja Matthee [a,*], Boris R. Krasnov [b]

[a] Department of Conservation Ecology and Entomology, Centre for Invasion Biology, Stellenbosch University, Private Bag X1, Stellenbosch, Western Cape 7602, South Africa
[b] Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel

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ABSTRACT

We studied abundance and distribution of seven ectoparasite species (fleas *Chiastopsylla rossi* and *Dynopsyllus ellobius*, a louse *Polyplax arvicanthis*, mites *Androlaelaps fahrenholzi* and *Laelaps giganteus* and two ticks *Haemaphysalis elliptica* and *Hyalomma truncatum*) exploiting the same populations of the rodent host *Rhabdomys pumilio* in South Africa. We considered three general patterns of abundance and distribution, namely (i) aggregated distribution of parasites amongst individual hosts; (ii) positive relationships between mean parasite abundance and their prevalence; and (iii) applicability of a simple epidemiological model based on mean parasite abundance and its variance to predict the observed patterns of prevalence. Our aims were to evaluate the relative role of host- versus parasite-associated factors by looking at similarity amongst different parasites in these patterns. In general, all parasites demonstrated strong similarity in each of the three patterns of abundance and distribution. However, the strength of these patterns differed amongst parasite species. We conclude that these patterns are driven mainly by hosts, but differences are caused by differences between various life-history traits of parasite species. Our results support the idea that general laws apply to parasite population ecology.

1. Introduction

Although the ecology of parasites is a relatively young discipline, it is rapidly developing and large quantities of data have been collected during recent decades (Combes, 2001; Poulin, 2007a). In particular, patterns of abundance and distribution have been investigated in a variety of parasite taxa exploiting various hosts in varying environments and in different geographic regions. Parasitism has evolved independently in many animal taxa. As a result, parasites are different in their life histories and strategies of host exploitation. Consequently, the question about the generality of patterns observed in different parasites still remains one of the crucial problems in parasite ecology. For example, almost four decades ago, Crofton (1971) had already proposed that an aggregated distribution of parasites amongst their hosts should be considered as a characteristic feature of parasitism because this pattern was widely observed amongst different parasites exploiting different hosts. This idea was further substantiated by a number of seminal papers (Anderson and May, 1978; Shaw and Dobson, 1995). In a recent review, Poulin (2007b) demonstrated that not only the aggregation of parasites amongst host individuals, but other patterns of abundance and distribution (e.g., positive relationship between prevalence and mean abundance of parasites) are strikingly similar in different parasite taxa.

Most studies in the long history of investigating patterns of parasite abundance and distribution have been either restricted to one parasite taxon (e.g., Godfrey et al., 2006) or based on meta-analyses of patterns found in different parasites exploiting different hosts in different locations and/or times (e.g., Shaw and Dobson, 1995). Comparisons of patterns of abundance and distribution amongst different parasites exploiting the same host from the same population(s) (i.e., in the same locations at the same time) have been undertaken more rarely (Haukisalmi, 1986; Boag et al., 2001; Newey et al., 2005; Poulin and Dick, 2007; Seifertová et al., 2008). Such comparisons may not only further validate the universality of abundance and distribution patterns and give insights into the scale-dependence of this universality, but may also allow evaluation of the relative role of host- versus parasite-associated factors that generate these patterns.

A number of factors driving each universal pattern have been suggested (Anderson and May, 1978; Shaw and Dobson, 1995; Poulin, 2007a,b). Essentially, these factors can be divided into two groups, namely host-related and parasite-related factors. For example, aggregated distribution of parasites may be caused by, on the one hand, heterogeneity of hosts in the face of parasitism, or, on

* Corresponding author. Tel.: +27 21 808 4777; fax: +27 21 808 3304.
E-mail addresses: smatthee@sun.ac.za (S. Matthee), krasnov@bgu.ac.il (B.R. Krasnov).

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the other hand, by stochastic demographic processes in parasite populations and/or the effect of mating probability of a parasite (Anderson and Gordon, 1982; Poulin, 2007a). Host-related factors have been suggested to be more important in generating the universal aggregative pattern of parasite distribution than the parasite-related mechanism (see reviews in Wilson et al., 2001 and Poulin, 2007a), although, to the best of our knowledge, this has never been tested specifically. If patterns of abundance and distribution are similar amongst different parasites exploiting the same hosts then, most likely, these patterns are governed by some features of host biology. If, however, these patterns are produced by parasite-related processes, then they would be likely to differ amongst parasites that showed differences in their behaviour. Furthermore, if the main trend of a pattern is similar in different parasites, but these parasites differ in the strength of the pattern, then these differences are likely to be produced by amongst-parasite differences in life-history. For example, whilst all parasites appear to be aggregated, considerable differences are observed in the degree of aggregation between parasite species or populations, and the causes of these differences are not well understood (Morand and Krasnov, 2008).

We studied the abundance and distribution of different ectoparasites exploiting the same rodent host, *Rhabdomys pumilio*, in the Western Cape Province of South Africa. These parasites belong to different arthropod taxa, namely fleas (Insecta: Siphonaptera), lice (Insecta: Phthiraptera), mites (Acari: Parasitiformes) and ticks (Acari: Parasitiformes). The four taxa vary with respect to life-history and the length of time spent on the host. Lice are permanent parasites, they reproduce directly on the host and transmission takes place through direct contact, whereas fleas, mites and ticks usually do not reproduce on the host. Fleas and mites are generally associated with the nest of the host and periodically attach to the host to obtain food and/or for dispersal (Marshall, 1981; Radovsky, 1985). Engorged ticks drop off the host and re-emerge after development to the next stage, on the vegetation in close proximity to the point of drop-off (Sonenshine, 1993).

We considered three general patterns of abundance and distribution that have been reported earlier for some, but not all of these taxa as follows. Firstly, we considered aggregated distribution of parasites amongst individual hosts and tested whether the degree of aggregation is similar between parasites. Earlier, aggregated distribution has been demonstrated for fleas (Krasnov et al., 2002), lice (Shaw et al., 1998; Qian et al., 2004), mites (Guo, 1997) and ticks (Randolph, 1995; Randolph et al., 1999; Nava et al., 2006) as well as for numerous other parasite taxa. Second, we searched for a positive relationship between local parasite abundance (mean number of parasites per individual host) and their prevalence. This relationship was suggested to be a reflection of one of the most pervasive macroecological patterns, namely, the positive relationship between local abundance and occupancy (Gaston, 2003). In the application of this relationship to host–parasite systems, a positive correlation between mean abundance and prevalence has been confirmed for nematodes (Morand and Guégan, 2000), monogeneans (Simkova et al., 2002) and fleas (Krasnov et al., 2005a). The explanation for this pattern may be straightforward. The probability that a parasite infests a new host individual is higher when the mean abundance of the parasite is higher. Third, we tested whether a simple epidemiological model based on mean parasite abundance and its variance can predict the observed patterns of prevalence. It has been shown that up to 96% of variance in flea (Krasnov et al., 2005a,b) and tick (Stanko et al., 2007) prevalence can be explained solely by their mean abundance, so there was no need to invoke more complex factors for the explanation of the variation in parasite prevalence.

2. Materials and methods

2.1. Study area and sampling

The striped mouse, *R. pumilio*, is one of the most abundant rodents in southern Africa. It occupies a variety of habitats and is a host for numerous ecto- and endoparasite species (De Graaf, 1981; Matthee et al., 2007). We captured *R. pumilio* in 2003–2004 at nine localities in the Western Cape Province of South Africa. The localities included five pristine lowland Fynbos/Renosterveld regions and four bordering agricultural areas (Matthee et al., 2007). Seven localities were sampled once, mainly during the breeding season, whereas two remaining localities were sampled four times with 3–4 month intervals between trapping sessions. Nevertheless, we considered each trapping session as independent because animals captured during each session were sacrificed (see below). Rodents were captured using Sherman-type live traps (90–180 traps per locality) baited with peanut butter and oats. A trapping session in each locality lasted 3–12 days. Parasites were collected from adult rodents, i.e. individuals with a body mass of more than 40 g. These animals were euthanised with Fluothane, placed in an individual pre-marked plastic bag and transferred to a laboratory where each animal was systematically examined under a stereoscopic microscope. All ectoparasites found were removed using forceps, counted and identified to species level. A total of 510 individuals of *R. pumilio* were trapped (24–57 animals per locality) from which eight flea species, one louse species, 11 mite species and 13 ixodid tick species were identified. In the analysis we included seven ectoparasite species that were either most abundant or recorded in at least five trapping sessions. These were two fleas (*Chiastopsylla rossi* and *Dynopsyllus ellobius*), a louse (*Polyplax arvicanthis*), two mites (*Androlaelaps fahrenholzi* and *Laelaps giganteus*) and two ticks (*Haemaphysalis elliptica* and *Hyalomma truncatum*).

2.2. Data analysis

We calculated mean abundance (mean number of parasites per host individual; M), variance of abundance (V) and prevalence (proportion of infested host individuals; P) for each trapping survey for each of seven parasite species. We evaluated the degree of aggregation of each parasite species amongst host individuals using the empirical relationship known as Taylor's power law (Taylor, 1961). According to this law, mean abundance of a species is related to variance of abundance as $V = aM^b$. The exponent (parameter b or slope of Taylor's relationship) of this function usually varies amongst species as $1 < b < 2$ (Kilpatrick and Ives, 2003). For parasites, it has been shown to be an inverse indicator of parasite-induced host mortality (Anderson and Gordon, 1982). An increase in b suggests that at least some of the hosts are infected with heavy burdens of parasites and it is commonly used as a measure of parasite aggregation (Perry, 1988; Shaw and Dobson, 1995; Morand and Guégan, 2000; Simkova et al., 2002; Krasnov et al., 2005a; Morand and Krasnov, 2008). We regressed log-transformed variance of parasite abundance against log-transformed mean of parasite abundance (both calculated within a trapping survey) and used t-tests to test whether the slope differs significantly from 1. To avoid an inflated Type I error, we applied a Bonferroni adjustment of α-level which resulted in $\alpha = 0.007$. We then compared amongst slopes of the resulting relationships using ANCOVA. We ran an ANCOVA across all parasites with a parasite species or parasite higher taxon (fleas, louse, mites and ticks) as a categorical predictor, then we ran ANCOVAs separately within fleas, mites and ticks.

To estimate the proportion of variance in parasite prevalence explained by their mean abundances, we fitted the observed rela-

tionship between prevalence and log mean abundance to the logistic curve. It has been shown that a logistic curve fits an empirical relationship between the fraction of sites where a given species occurs (prevalence) and its mean abundance (Gaston, 1999). We applied least squares estimation procedures via the Levenberg-Marquardt algorithm (Moré, 1977). We used *t*-tests to test for between-species differences in the slopes of the logistic fit.

To test whether simple epidemiological models predict prevalence of different parasites equally well, we used the model suggested by Anderson and May (1985). According to this model, the prevalence of infection P at any given time and the mean abundance of parasites M are related as $P = 1 - (1 + M/k)^{-k}$, where k is the parameter of the negative binomial distribution inversely indicating degree of aggregation (Morand and Guégan, 2000; Krasnov et al., 2005a, b; Stanko et al., 2007). We estimated k using two methods. We used parameters a and b of Taylor's power law (Taylor et al., 1979) as $1/k = aM^{b-2} - 1/M$, and we used the moment estimate of Elliot (1977), corrected for sample size as $k = (M^2 - V/n)/(V - M)$, where M is mean abundance, V is variance of abundance and n is host sample size. We then calculated the expected prevalences (P_{expT} and P_{expE}, respectively) for each parasite across trapping sessions and compared each of those with the observed prevalence using linear regression. We used *t*-tests to test whether the slopes of the resulted regressions differed significantly from unity.

3. Results

The slope of the relationship between log-transformed variance and mean abundance of parasites was significantly greater than unity in all parasite species, except for a flea *D. ellobius* ($t = 4.6 - 8.5$, $P < 0.001$ for all; Table 1; see Fig. 1 for illustrative examples with a flea, *C. rossi*, and a tick, *H. elliptica*). In one case (*D. ellobius*), a slope of log variance against log mean abundance was significantly lower than 1 ($t = -3.5$; $P < 0.001$). Slopes of other regressions of log-transformed variances against log-transformed mean abundances varied from the lowest in a flea, *C. rossi*, to the highest in a louse, *P. arvicanthis*. This highest slope indicated that the louse, *P. arvicanthis*, was the most aggregated compared to the other species. The results of ANCOVA demonstrated a significant interaction between continuous and categorical predictors independently of whether the categorical predictor was a parasite species or a higher parasite taxon ($F_{6,85} = 5.4$ and $F_{6,85} = 5.5$, respectively; $P < 0.001$ for both) suggesting significant differences amongst parasite species or higher taxa in the degree of their aggregation. Furthermore, when ANCOVAs were run within a higher parasite taxon, it appeared that no significant difference in the degree of aggregation occurred between two mites ($F_{2,26} = 5.4$, $P = 0.10$) and two ticks ($F_{2,17} = 0.9$, $P = 0.35$), whereas two fleas differed significantly in their degree of aggregation ($F_{1,20} = 7.5$, $P < 0.01$).

The relationship between the prevalence of each parasite and its mean abundance fitted the logistic curve (Table 2; see Fig. 2 for illustrative examples with a louse, *P. arvicanthis* and a mite, *L. giganteus*). In general, prevalences were low at low parasite abundances (as in Shaw and Dobson (1995)) and rose rapidly to high asymptotes with an increase in abundances (although the rate of the rise varied between parasites). The slowest increase in prevalence with an increase in mean abundance occurred in a louse, *P. arvicanthis* (further indicating that this parasite demonstrated the highest degree of aggregation), whereas the steepest increase occurred in a mite, *L. giganteus*. No significant differences between slopes of logistic fit were found between different fleas, mites or ticks ($t = 0.96$, $t = 1.17$ and $t = 1.75$, respectively; $P > 0.10$ for all). Prevalences of *P. arvicanthis* and both ticks increased with increases in their mean abundance at a considerably slower rate than were the cases in both fleas ($t = 2.26 - 2.62$, $P < 0.05$).

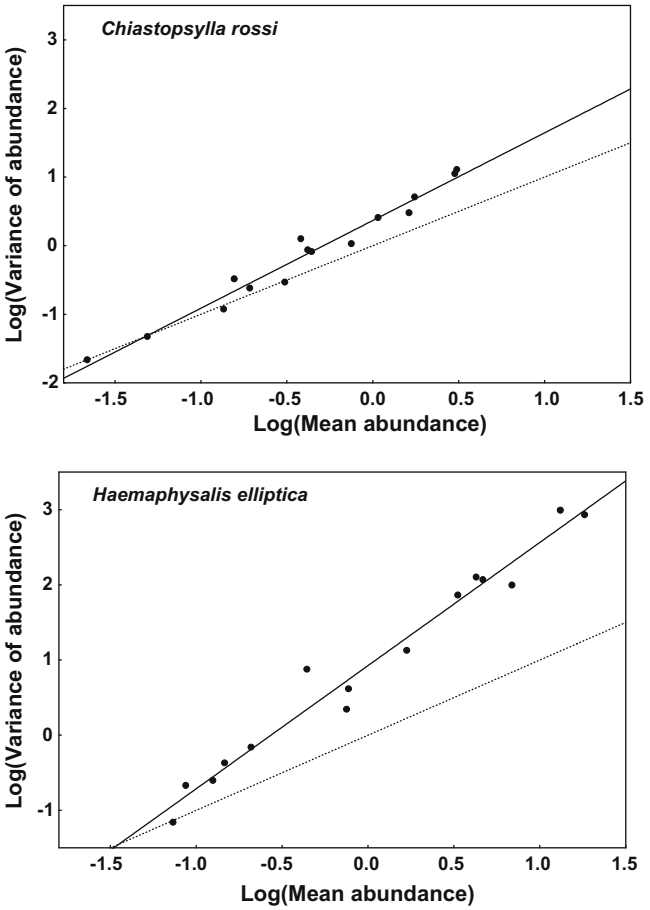

Fig. 1. Relationship between log variance of abundance and log mean abundance of a flea *Chiastopsylla rossi* and a tick *Haemophysalis elliptica* parasitic on *Rhabdomys pumilio*. Dashed lines have slopes equal to 1.

Table 1
Summary of regression analyses of relationships between log variance and log mean abundance of seven parasites of *Rhabdomys pumilio* ($P < 0.001$ for all cases).

Parasite	Identities	Intercept ($\log a$) ± S.E.	Slope (b) ± S.E.	r^2	Degrees of freedom	*F*-test statistics
Chiastopsylla rossi	Flea	0.37 ± 0.04	1.28 ± 0.06	0.97	1,13	402.2
Dynopsyllus ellobius	Flea	−0.10 ± 0.03	0.93 ± 0.02*	0.99	1,7	1807.2
Polyplax arvicanthis	Louse	0.59 ± 0.08	1.73 ± 0.11	0.95	1,13	231.5
Laelaps giganteus	Mite	0.54 ± 0.04	1.39 ± 0.07	0.97	1,13	417.1
Androlaelaps fahrenholzi	Mite	0.52 ± 0.07	1.66 ± 0.14	0.91	1,13	135.8
Haemophysalis elliptica	Tick	0.92 ± 0.06	1.64 ± 0.07	0.97	1,13	444.5
Hyalomma truncatum	Tick	0.60 ± 0.07	1.66 ± 0.08	0.99	1,4	379.3

Intercepts are significant, $P < 0.001$. Slopes, except marked by *, are significantly greater than 1, slope marked by * is significantly lower than 1 (see text for *t*-values and explanations).

Table 2
Summary of fitting logistic function to the relationships between prevalence and log mean abundance of seven parasites of *Rhabdomys pumilio*.

Parasite	Variance explained (%)	*r*	Intercept ± S.E.	Slope ± S.E.	*F*-test statistics
Chiastopsylla rossi	0.97	0.99	0.12 ± 0.07*	2.86 ± 0.20	689.9
Dynopsyllus ellobius	0.99	0.99	0.46 ± 0.03	2.63 ± 0.04	13,063.8
Polyplax arvicanthis	0.75	0.87	−0.46 ± 0.22*	1.66 ± 0.33	161.2
Laelaps giganteus	0.92	0.96	−0.47 ± 0.12	2.99 ± 0.35	286.7
Androlaelaps fahrenholzi	0.84	0.92	−0.17 ± 0.14*	2.17 ± 0.35	228.5
Haemophysalis elliptica	0.91	0.96	−1.08 ± 0.17	1.77 ± 0.23	191.5
Hyalomma truncatum	0.93	0.96	−0.21 ± 0.29*	1.89 ± 0.29	163.7

All regressions are significant, $P < 0.001$. Parameters not marked by * are significant, $P < 0.001$.

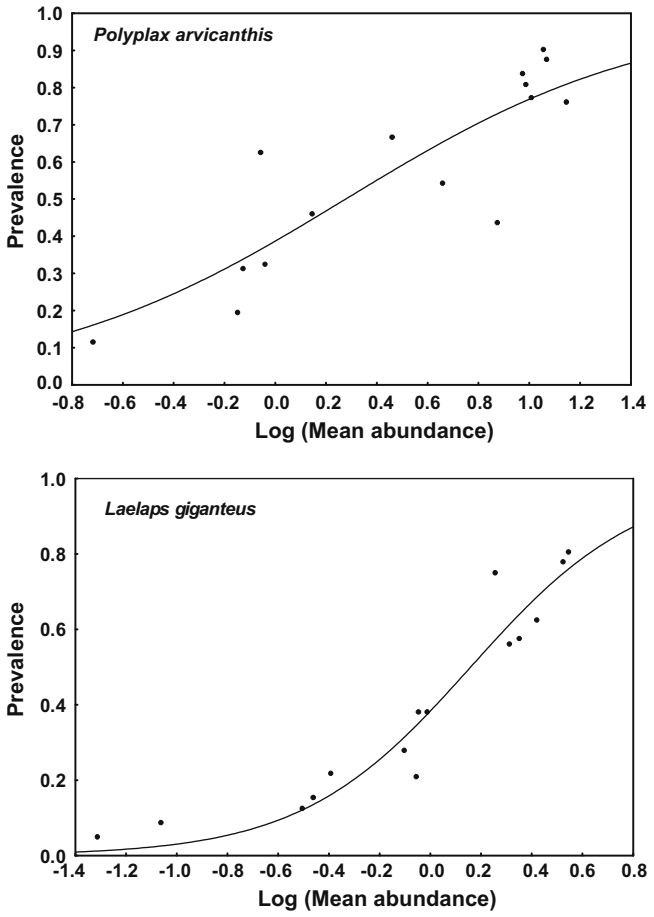

Fig. 2. Logistic function fit for prevalence of a louse *Polyplax arvicanthis* and a mite *Laelaps giganteus* parasitic on *Rhabdomys pumilio*.

Whatever the method of estimation of *k* used, epidemiological models successfully predicted prevalences in some parasites (*D. ellobius*, *P. arvicanthis* and *H. truncatum*) ($t = -1.92 - -0.64$; $P > 0.05$ for all), whereas they consistently underestimated prevalences in other parasites (*C. rossi*, *A. fahrenholzi* and *H. elliptica*) ($t = -2.11 - -4.00$; $P < 0.007$ for all) (Table 3; see Fig. 3 for illustrative examples with fleas, *D. ellobius* and *C. rossi*). In the case of a mite, *L. giganteus*, the model with *k* calculated using Taylor's power law underestimated prevalences ($t = -2.57$, $P < 0.007$), whereas the model with the moment estimate of *k* predicted prevalence adequately ($t = -1.57$, $P > 0.05$) (Fig. 4).

4. Discussion

In general, different ectoparasites exploiting the same host at the same time in the same localities demonstrated a strong similarity in each of the three studied patterns of abundance and distribution. Indeed, (i) six of the seven ectoparasites (except *D. ellobius*) were aggregated amongst host individuals, (ii) all the ectoparasites showed a significant positive relationship between abundance and occupancy (prevalence) which was adequately described by a logistic fit and (iii) a simple epidemiological model that incorporated aggregation as a variable successfully predicted observed prevalence for several different ectoparasites. These results support the idea of Poulin (2007b) that general laws apply to most parasites when they are considered at the population level. Furthermore, Poulin's (2007b) idea was the outcome of a meta-analysis of various studies of various hosts in a variety of geographic regions, i.e. at the macro-scale. Our results validate this idea at a relatively small scale and critically, within a single host species.

On the other hand, some between-species and amongst-higher taxon variability in the strength of these patterns was found. In particular, the degree of aggregation and slopes of the logistic fit differed between higher taxa of ectoparasites. A simple epidemiological model incorporating aggregation successfully predicted prevalence in one flea (*D. ellobius*), a louse and one tick (*H. truncatum*), whereas successful prediction of prevalence of one mite (*L. giganteus*) required an additional parameter (host number) in the model. In contrast, the model consistently underestimated prevalences in the remaining ectoparasites (*C. rossi*, *A. fahrenholzi*, and *H. elliptica*). Below we will discuss the reasons for universality and possible causes of amongst-parasite variability of appearance for each of these patterns.

Parasites studied here differ in their origin, physiology, life cycle and behaviour. However, they exploit the same hosts at the same time and in the same localities. Strong similarity of the patterns of abundance and distribution amongst these ectoparasites thus suggest that these patterns are driven mainly by hosts, whereas the differences amongst parasites indicate an important role of parasite life histories. Nevertheless, despite their taxonomic difference, parasites considered in our study share several important biological features (haematophagy, adaptations to anchor themselves to the skin of a host). These shared features may also have a role in the amongst-parasite similarity of the observed patterns.

The causes of aggregated distribution in parasites have been discussed extensively (Anderson and May, 1978; Shaw and Dobson, 1995; Shaw et al., 1998; Combes, 2001; Wilson et al., 2001; Poulin, 2007a). Our results are consistent with, but do not explicitly prove, that parasite aggregation arises mainly due to inequality of hosts in the face of parasitism. In other words, different host individuals differ in their suitability for parasites which may stem from amongst-host variation in (i) quantity and quality of host resources and (ii) the pattern of resource acquisition by a parasite (such as probability of encountering a host or host defence ability). The suitability of a host for parasite infection may thus depend on a variety of host-related factors such as sex, age, reproductive status and nutritional status. For example, androgens, specifically testosterone, can facilitate higher parasite loads in male mice (Schalk and Forbes, 1997; Hughes and Randolph, 2001; Moore and Wilson,

Table 3
Summary of regressions of prevalences expected from the epidemiological models (P_{expT} and P_{expE}) against observed prevalences for seven parasites of *Rhabdomys pumilio*.

Parasite	Slope P_{expT}±S.E.	r^2	F	Slope P_{expE}±S.E.	r^2	F-test statistics
Chiastopsylla rossi	0.91 ± 0.04	0.98	523.4	0.88 ± 0.03	0.99	785.2
Dynopsyllus ellobius	0.94 ± 0.07*	0.99	16166.0	0.98 ± 0.02*	0.99	20.7
Polyplax arvicanthis	0.77 ± 0.12*	0.75	39.5	0.87 ± 0.08*	0.89	106.4
Laelaps giganteus	0.82 ± 0.07	0.92	148.5	0.89 ± 0.07*	0.93	173.9
Androlaelaps fahrenholzi	0.74 ± 0.09	0.82	59.9	0.81 ± 0.09	0.85	73.3
Haemophysalis elliptica	0.85 ± 0.07	0.92	147.9	0.89 ± 0.05	0.96	261.5
Hyalomma truncatum	0.86 ± 0.13*	0.96	46.9	0.91 ± 0.14*	0.92	44.2

All regressions and slopes are significant, $P < 0.001$. Slopes not marked by * significantly differ from 1 (t-tests, $P < 0.05$; see text for t-values and explanations). All intercepts are not significant and, consequently, are not shown. k values for P_{expT} and P_{expE} were calculated using either Taylor's power law or corrected for host number moment estimate, respectively.

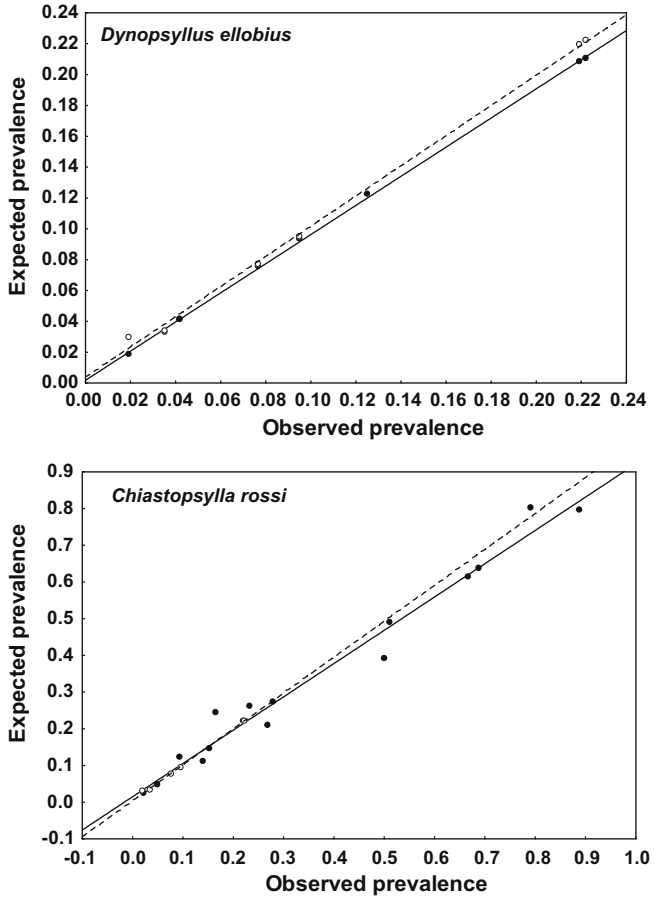

Fig. 3. Relationship between observed and expected (from the epidemiological models, with different k estimation) prevalence of fleas *Dynopsyllus ellobius* and *Chiastopsilla rossi* parasitic on *Rhabdomys pumilio*. P_{expT} – closed circles, solid line; P_{expE} – open circles, dashed line. See text for explanations (Section 2.2).

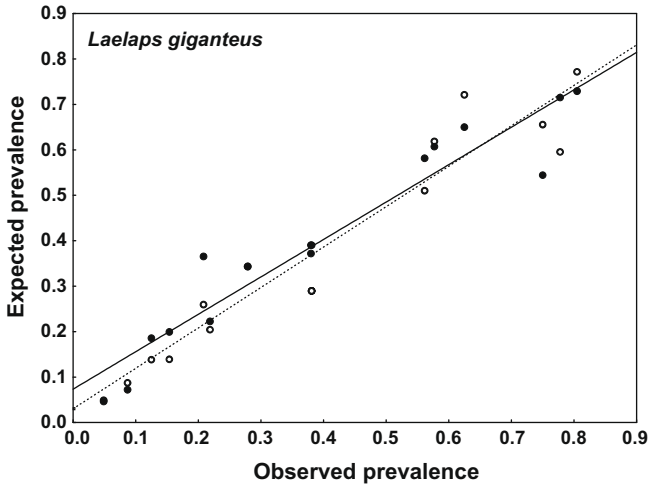

Fig. 4. Relationship between observed and expected (from the epidemiological models, with different k estimation) prevalence of a mite *Laelaps giganteus* parasitic on *Rhabdomys pumilio*. P_{expT} – closed circles, solid line; P_{expE} – open circles, dashed line. See text for explanations (Section 2.2).

2002; Cox and John-Alder, 2007). Body size often increases with age and larger animals may be able to tolerate larger parasite burdens (Schalk and Forbes, 1997; Moore and Wilson, 2002). Host behaviour can also contribute to heterogeneity in susceptibility to infection. Males with larger home ranges or those that spend more time patrolling an area may have more parasites compared with females as a result of increased exposure and contact rate with parasites that occur in the vegetation (Bandilla et al., 2005). In addition, participation in allogrooming (grooming group members) and autogrooming (self-grooming) activities by group members can result in fewer permanent parasites, such as lice (Marshall, 1981). Host body condition can also play a contributing role as malnutrition not only leads to a decrease in plasma glucose concentration (De Pedro et al., 2003) but also to weakening of the defence means of a host (Saino et al., 1997). Empirical studies that test host-related factors in *R. pumilio* populations are lacking. However, it is predicted that testosterone is an important factor mainly due to the fact that approximately 70% of the males in our study were in breeding condition (Schradin, 2008). Exposure rate as a consequence of larger home range size may also contribute to higher parasite loads on males compared with females. A study on *R. pumilio* in the more xeric succulent karoo habitat indicated that breeding males spend more time patrolling their territories, whilst females forage more frequently closer to the nest (Schradin, 2006). There appears to be no evidence of the role of sexual size dimorphism as males were not significantly larger than females (S. Matthee, unpublished data).

Although all ectoparasites, except *D. ellobius*, demonstrated an aggregative pattern of distribution, the higher parasite taxa differed in the degree of their aggregation as indicated by significant differences in the values of the slope of Taylor's power relationships. The reason for this difference in the appearance of a general pattern is that, although aggregative distribution is a general characteristic of parasites, the degree of aggregation varies amongst parasite species within limits (Krasnov et al., 2006a). These limits seem to depend on some species-specific traits (Krasnov et al., 2005a, 2006a). For example, lower variability of abundant populations compared with scarce populations implies the increasing intensity and/or efficiency of processes of population regulation with increasing abundance (less increase in variability with increasing abundance). A difference in the slope of Taylor's rela-

tionship suggests that the level of abundance at which population regulation becomes efficient varies amongst species. The threshold of abundance at which population regulation starts may depend on some specific properties. Parasites face a trade-off between being too aggregated and being too randomly distributed (Anderson and Gordon, 1982; Shaw and Dobson, 1995). A parasite could be lost due to high mortality of overly infested hosts if the level of aggregation is too high, whereas a parasite's mating opportunities could be sharply decreased if its distribution across host individuals is random. Consequently, an optimal level of aggregation and a level of abundance at which regulation processes start to act seem to be species-specific and depend on demographic factors such as intrinsic birth and death rates, mating behaviour and mobility. Indeed, parasite species differ drastically in such traits as oviposition rate, clutch size and migration rate (Marshall, 1981; Krasnov, 2008). In addition, highly aggregated distributions could be promoted mechanistically. For example, in our study, the highest level of aggregation was found in the louse which belongs to the only ectoparasite taxon that directly reproduces on the host. Direct reproduction of a parasite on/in a host individual is one of the main parasite-associated causes of aggregation (Poulin, 2007b). Furthermore, this louse *P. arvicanthis* is specific to *R. pumilio* (Ledger, 1980). Highly host specific parasites are expected to be characterised by a higher degree of aggregation (Clayton and Tompkins, 1995; Krasnov et al., 2005a, 2006a). However, the distribution of a host-generalist mite such as *A. fahrenholzi* that reproduces off the host was also highly aggregated, suggesting that (i) aggregation may arise not only due to purely mechanistic reasons and (ii) that factors other than host-specificity may also be responsible for species-specific limits of aggregation.

The positive relationship between parasite abundance and prevalence is a manifestation of the general abundance–occupancy relationship of free-living organisms (Gaston, 1999, 2003). Positive abundance–occupancy relationships were explained using various hypotheses (Gaston, 2003), the most common being the sampling artifact hypothesis, the ecological specialisation hypothesis and the core-satellite hypothesis (Hanski et al., 1993). However, the sampling artifact hypothesis was rejected in studies of various parasite–host systems (Poulin, 1998; Morand and Guégan, 2000; Simkova et al., 2002; Krasnov et al., 2002), whereas the two latter hypotheses were supported for some but not other host–parasite associations (Morand and Guégan, 2000; Simkova et al., 2002; Krasnov et al., 2004, 2005a). It should be noted, however, that most of these studies considered interspecific rather than intraspecific abundance–occupancy relationships.

Whatever the mechanism behind the positive abundance–prevalence relationship may be, the most important findings in our study are that (i) a large proportion of the variance in parasite prevalence was explained solely by their mean abundance and (ii) this proportion differed amongst parasites belonging to different taxa. The differences in the proportion of variance in prevalence explained by mean abundance amongst parasite taxa may be associated with differences in dispersal abilities amongst these taxa. In other words, the higher the dispersal abilities of a parasite are, the higher proportion of variance in prevalence would be explained by mean abundance, and greater dispersal may lead to greater potential for increased prevalence. Ectoparasite colonisation of new host individuals may be passive (when host individuals come into direct contact with one another) or active (free dispersal). Obviously, in case of a passive colonisation (i.e., absence of free dispersal), the higher parasite abundance on a parasite donor would lead to a higher probability of infestation of a parasite recipient. However, given the aggregated distribution of parasites (i.e., small number of highly infested individuals), the portion of variance in prevalence explained by mean abundance is expected to be low. In the case of active colonisation, the higher parasite abundance would lead to a higher probability of a previously uninfested host being attacked by parasites. Indeed, the highest proportion of variance in prevalence was explained by the mean abundance in fleas (which are able to quest for a host actively; Krasnov, 2008), followed by that in ticks (which prefer the strategy of a sit-and-wait predator; Sonenshine, 1993), whereas the lowest proportion of variance in prevalence was explained by mean abundance in the louse (in which the ability to disperse freely is lacking).

Our study demonstrated that a simple epidemiological model that takes into account two main parameters, namely mean abundance and its variance, can be successfully applied to a wide range of parasite taxa that vary with respect to (i) tightness of their association with hosts and (ii) life-history, thus validating earlier results (Morand and Guégan, 2000; Krasnov et al., 2005a,b; Stanko et al., 2007). The ability of this model to successfully predict prevalence demonstrates the sufficiency of the most parsimonious set of factors to explain much of the variance in prevalence without involving complicated mechanisms such as the degree of host specificity and the level of host resistance.

Nevertheless, although the model accurately predicted observed prevalence in the flea *D. ellobius*, the louse *P. arvicanthis* and the tick *H. truncatum*, it consistently underestimated prevalences in the flea *C. rossi*, the mite *A. fahrenholzi*, and the tick *H. elliptica*. In other words, there were more individuals of *R. pumilio* infested with *C. rossi*, *A. fahrenholzi* and *H. elliptica* than predicted with the model. In addition, the model successfully predicted prevalence in the mite *L. giganteus* only when it was corrected for host sample size.

The between-parasite within-higher taxon differences suggest that some feature of the life-history of a species may affect the applicability of the model. For example, although all ticks spend a larger part of their life cycle off the host, they vary in the tightness of their association with a host. For example, *H. elliptica* has a three-host life cycle with larvae dropping off the host after engorgement and moulting in the external environment into nymphs that then have to find the next host (Howell et al., 1978). In contrast, *H. truncatum* has a two-host life cycle with larvae staying on the host after engorgement and moulting on the host into nymphs that reattaches to the same host individual (Howell et al., 1978). In other words, the association with a host is obviously tighter in the latter species than in the former species. Presumably as a result, the accuracy of a simple model in the prediction of prevalence is higher for *H. truncatum* than for *H. elliptica*. The lack of detailed knowledge of life-history of the particular flea and mite species does not allow us to suggest similar explanations for between-flea and between-mite differences.

Earlier, the difference in the applicability of this model to different species inhabiting different geographic regions was explained by differences in the environmental predictability (Krasnov et al., 2005a,b). The results of our study suggest that life-history differences between species are more important and that the applicability of the model may vary not only geographically but also amongst parasites within the same region.

Although the results of many studies (Combes, 2001; Wilson et al., 2001; Poulin, 2007a) suggest that parasite dynamics are driven mainly by mechanisms acting within a host and/or within a parasite, there is an increasing body of empirical evidence indicating that interactions between parasites may be partly responsible for at least some patterns of abundance. For example, the level of interspecific aggregation in assemblages of ectoparasites of fish (Morand et al., 1999; Simkova et al., 2000) and mammals (Krasnov et al., 2006b) was reduced in relation to the level of intraspecific aggregation, facilitating the co-existence of multiple parasite species. Lello et al. (2004) demonstrated that either direct or indirect interactions mediated via the host immune system between intestinal helminths of free-ranging rabbits may result in changes in abundance of the interacting species. Although not widespread, this

evidence indicates that the effect of interspecific parasite interactions within host individuals on the patterns of abundance and distribution of parasites within a host population deserves special investigation.

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References

Anderson, R.M., Gordon, D.M., 1982. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortality. Parasitology 85, 373–398.

Anderson, R.M., May, R.M., 1978. Regulation and stability of host–parasite population interactions. I. Regulatory processes. J. Anim. Ecol. 47, 219–247.

Anderson, R.M., May, R.M., 1985. Helminth infections of humans: mathematical models, population dynamics and control. Adv. Parasitol. 24, 1–101.

Bandilla, M., Hakalahti, T., Hudson, P.J., Valtonen, E.T., 2005. Aggregation of *Argulus coregoni* (Crustacea: Branchiura) on rainbow trout (*Oncorhynchus mykiss*): a consequence of host susceptibility or exposure? Parasitology 130, 169–176.

Boag, B., Lello, J., Fenton, A., Tompkins, D.M., Hudson, P.J., 2001. Pattarens of parasite aggregation in the wild European rabbit (*Oryctolagus cuniculus*). Int. J. Parasitol. 31, 1421–1428.

Clayton, D.H., Tompkins, D.M., 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). Parasitology 110, 195–206.

Combes, C., 2001. Parasitism. The Ecology and Evolution of Intimate Interactions. University of Chicago Press, Chicago and London.

Cox, R.M., John-Alder, H.B., 2007. Increased mite parasitism as a cost of testosterone in male striped plateau lizards *Sceloporus virgatus*. Funct. Ecol. 21, 327–334.

Crofton, H.D., 1971. A quantitative approach to parasitism. Parasitology 62, 179–193.

De Graaf, G., 1981. The Rodents of Southern Africa. Butterworths, Durban, South Africa.

De Pedro, N., Delgado, M.J., Gancedo, B., Alonso-Bedate, M., 2003. Changes in glucose, glycogen, thyroid activity and hypothalamic catecholamines in tench by starvation and refeeding. J. Comp. Physiol. B. 173, 475–481.

Elliot, J.M., 1977. Some Methods for Statistical Analysis of Samples of Benthic Invertebrates, 2nd Edn. Freshwater Biological Association Sceintific Publications, No. 25, Titus Wilson and Son, Ambleside, UK.

Gaston, K.J., 1999. Implications of interspecific and intraspecific abundance–occupancy relationships. Oikos 86, 195–207.

Gaston, K.J., 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.

Godfrey, S.S., Bull, C.M., Murray, K., Gardner, M.G., 2006. Transmission mode and distribution of parasites among groups of the social lizard *Egernia stokesii*. Parasitol. Res. 99, 223–230.

Guo, X.-G., 1997. Spatial pattern analysis of *Laelaps echidninus* and *Laelaps nuttalli* using Iwao1s method and a significance test of random deviation (Acari: Laelapidae). Syst. Appl. Acarol. 2, 89–94.

Hanski, I., Kouki, J., Halkka, A., 1993. Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. Historical and Geographical Perspectives. University of Chicago Press, Chicago and London, pp. 108–116.

Haukisalmi, V., 1986. Frequency distribution of helminths in microtine rodents in Finnish Lapland. Ann. Zool. Fennici 23, 141–150.

Howell, C.J., Walker, J.B., Nevill, E.M., 1978. Ticks, Mites and Insects Infesting Domestic Animals in South Africa. Part 1. Descriptions and Biology. Department of Agricultural Technical Services, Pretoria (Science Bulletin No. 393).

Hughes, V.L., Randolph, S.E., 2001. Testosterone depresses innate and acquired resistance to ticks in natural rodent hosts: a force for aggregated distributions of parasites. J. Parasitol. 87, 49–54.

Kilpatrick, A.M., Ives, A.R., 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422, 65–68.

Krasnov, B.R., Khokhlova, I.S., Shenbrot, G.I., 2002. The effect of host density on ectoparasite distribution: an example with a desert rodent parasitized by fleas. Ecology 83, 164–175.

Krasnov, B.R., Poulin, R., Shenbrot, G.I., Mouillot, D., Khokhlova, I.S., 2004. Ectoparasitic "jacks-of-all-trades": relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. Amer. Nat. 164, 506–515.

Krasnov, B.R., Morand, S., Khokhlova, I.S., Shenbrot, G.I., Hawlena, H., 2005a. Abundance and distribution of fleas on desert rodents: linking Taylor's power law to ecological specialization and epidemiology. Parasitology 131, 825–837.

Krasnov, B.R., Stanko, M., Miklisova, D., Morand, S., 2005b. Distribution of fleas (Siphonaptera) among small mammals: mean abundance predicts prevalence via simple epidemiological model. Int. J. Parasitol. 35, 1097–1101.

Krasnov, B.R., Stanko, M., Miklisova, D., Morand, S., 2006a. Host specificity, parasite community size and the relation between abundance and its variance. Evol. Ecol. 20, 75–91.

Krasnov, B.R., Stanko, M., Khokhlova, I.S., Mosansky, L., Shenbrot, G.I., Hawlena, H., Morand, S., 2006b. Aggregation and species coexistence in fleas parasitic on small mammals. Ecography 29, 159–168.

Krasnov, B.R., 2008. Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology. Cambridge University Press, Cambridge.

Ledger, J.A., 1980. The arthropod parasites of vertebrates in Africa south of the Sahara. In: Phthiraptera (Insecta). Vol. IV. Publications of the South African Institute for Medical Research No. 56. South African Institute for Medical Research, Johannesburg, South Africa.

Lello, J., Boag, B., Fenton, A., Stevenson, I.R., Hudson, P.J., 2004. Competition and mutualism among the gut helminths of a mammalian host. Nature 428, 840–844.

Marshall, A.G., 1981. The Ecology of Ectoparasitic Insects. Academic Press, London.

Matthee, S., Horak, I.G., Beaucournu, J.-C., Durden, L.A., Ueckermann, E.A., McGeoch, M.A., 2007. Epifaunistic arthropod parasites of the four-striped mouse, *Rhabdomys pumilio*, in the Western Cape Province, South Africa. J. Parasitol. 93, 47–59.

Morand, S., Guégan, J.-F., 2000. Distribution and abundance of parasite nematodes: ecological specialization, phylogenetic constraints or simply epidemiology? Oikos 88, 563–573.

Morand, S., Krasnov, B.R., 2008. Why apply ecological laws to epidemiology? Trends Parasitol. 24, 304–309.

Morand, S., Poulin, R., Rohde, K., Hayward, C., 1999. Aggregation and species coexistence of ectoparasites of marine fish. Int. J. Parasitol. 29, 663–672.

Moré, J., 1977. The Levenberg-Marquardt algorithm: implementation and theory. In: Watson, G.A. (Ed.), Numerical Analysis. Springer-Verlag, NY, pp. 105–116.

Moore, S.L., Wilson, K., 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297, 2015–2018.

Nava, S., Mangold, A.J., Guglieimone, A.A., 2006. The natural hosts of larvae and nymphs of *Amblyomma tigrinum* Kohh, 1844 (Acari: Ixodidae). Vet. Parasitol. 140, 124–132.

Newey, S., Shaw, D.J., Kirby, A., Montieth, P., Hudson, P.J., Thirgood, S.J., 2005. Prevalence, intensity and aggregation of intestinal parasites in mountain hares and their potential impact on population dynamics. Int. J. Parasitol. 35, 367–373.

Perry, J.N., 1988. Some models for spatial variability of animal species. Oikos 51, 124–130.

Poulin, R., 1998. Large-scale patterns of host use by parasites of freshwater fishes. Ecol. Lett. 1, 118–128.

Poulin, R., 2007a. Evolutionary Ecology of Parasites: From Individuals to Communities. Princeton University Press, Princeton.

Poulin, R., 2007b. Are there general laws in parasite ecology? Parasitology 134, 763–776.

Poulin, R., Dick, T.A., 2007. Spatial variation in population density across the geographical range in helminth parasites of yellow perch, *Perca flavescens*. Ecography 30, 629–636.

Qian, T.J., Guo, X.G., Guo, L.J., Zhang, L., Ma, Z.M., Li, W., 2004. Investigation and analysis of sucking lice on the body surface of *Rattus flavipectus*. Chinese J. Parasit. Dis. Cont. 17, 71–74 (in Chinese).

Radovsky, F.J., 1985. Evolution of mammalian mesostigmatid mites. In: Kim, K.C. (Ed.), Coevolution of Parasitic Arthropods and Mammals. John Wiley, New York, pp. 441–504.

Randolph, S.E., 1995. Patterns of the distribution of the tick *Ixodes trianguliceps* Birula on its host. J. Anim. Ecol. 44, 451–474.

Randolph, S.E., Miklisova, D., Lysy, J., Rogers, D.J., Labuda, M., 1999. Incidence from coincidence: patterns of tick infestation on rodents facilitate transmission of tick-borne encephalitis virus. Parasitology 118, 177–186.

Saino, N., Calza, S., Møller, A.P., 1997. Immunocompetence of nestling barn swallows in relation to brood size and parental effort. J. Anim. Ecol. 66, 827–836.

Schalk, G., Forbes, M.R., 1997. Male biases in parasitism of mammals: effects of study type, host age and parasite taxon. Oikos 78, 67–74.

Schradin, C., 2006. Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. J. Ethol. 24, 37–43.

Schradin, C., 2008. Seasonal changes in testosterone and corticosterone levels in four social classes of a desert dwelling sociable rodent. Horm. Behav. 53, 573–579.

Seifertová, M., Vyskočilová, M., Morand, S., Šimková, A., 2008. Metazoan parasites of freshwater cyprinid fish (*Leuciscus cephalus*): testing biogeographical hypotheses of species diversity. Parasitology 135, 1417–1435.

Shaw, D.J., Dobson, A.P., 1995. Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111, S111–S127.

Shaw, D.T., Grenfell, B.T., Dobson, A.P., 1998. Pattern of macroparasite aggregation in wildlife host populations. Parasitology 117, 597–610.

Simkova, A., Desdevises, Y., Gelnar, M., Morand, S., 2000. Co-existence of nine gill ectoparasites (*Dactylogyrus*: Monogenea) parasitizing the roach (*Rutilus rutilus* L.): history and present ecology. Int. J. Parasitol. 30, 1077–1088.

Simkova, A., Kadlec, D., Gelnar, M., Morand, S., 2002. Abundance–prevalence relationship of gill congeneric ectoparasites: testing the core satellite hypothesis and ecological specialization. Parasitol. Res. 88, 682–686.

Sonenshine, D.E., 1993. Biology of Ticks. Vol. 2. Part IV. Ecology, Behavior, and Host–Parasite Interactions. Oxford University Press, New York, New York.

Stanko, M., Krasnov, B.R., Miklisova, D., Morand, S., 2007. Simple epidemiological model predicts the relationships between prevalence and abundance in ixodid ticks. Parasitology 134, 59–68.

Taylor, L.R., 1961. Aggregation, variance and the mean. Nature 189, 732–735.

Taylor, L.R., Woiwod, I.P., Perry, J.N., 1979. The negative binomial as a dynamic ecological model and density-dependence of *k*. J. Anim. Ecol. 48, 289–304.

Wilson, K., Bjørnstad, O.N., Dobson, A.P., Merler, S., Poglaen, G., Randolph, S.E., Read, A.F., Skorping, A., 2001. Heterogeneities in macroparasite infections: patterns and processes. In: Hudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H., Dobson, A.P. (Eds.), The Ecology of Wildlife Diseases. Oxford University Press, Oxford, pp. 6–44.